

# Rhynchonycteris naso. By David L. Plumptre and J. Knox Jones, Jr.

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## Rhynchonycteris Peters, 1867

*Proboscidea* Spix, 1823:61. Type species *Proboscidea saxatilis* Spix (= *Vespertilio naso* Wied-Neuwied) by original designation. Not *Proboscidea* Brugière, 1791 (a nematode).

*Rhynchonycteris* Peters, 1867:477. Type species *Vespertilio naso* Wied-Neuwied by monotypy.

*Rhynchiscus* Miller, 1907b:65. Type species *Vespertilio naso* Wied-Neuwied by original designation. A renaming of *Rhynchonycteris* based on the assumption that the name was preoccupied by *Rhynchonycteris* Tschudi (see discussion by Husson, 1962: 35-36).

**CONTEXT AND CONTENT.** Order Chiroptera, Suborder Microchiroptera, Superfamily Emballonuroidea, Family Emballonuridae, Subfamily Emballonurinae. *Rhynchonycteris* is a monotypic genus.

## Rhynchonycteris naso (Wied-Neuwied, 1820)

### Brazilian Long-nosed Bat

*Vespertilio naso* Wied-Neuwied, 1820:251. Type locality "Die Ufer des Mucuri"; restricted to vicinity of Morro d'Arara, Rio Mucuri, Bahia, Brasil, by Avila-Pires (1965:9).

*Proboscidea saxatilis* Spix, 1823:62. Type locality "fluvem St. Francisci" [Rio São Francisco], Brasil.

*Proboscidea rivalis* Spix, 1823:62. Type locality "fluvem Amazonum" [Rio Amazonas], Brasil.

*Emballonura lineata* Temminck, 1841:297. Type locality "Surinam."

*Proboscidea villosa* Gervais, 1856:68. Type locality "la province de Goyaz," Brasil.

*Rhynchonycteris naso*: Peters, 1867:478. First use of current name combination.

**CONTEXT AND CONTENT.** Context as in generic account above. *R. naso* currently is regarded as a monotypic species, although a subspecific name, *Rhynchiscus naso priscus* Allen, 1914: 109, with type locality at "Xcopen, Quintana Roo, Mexico," once was applied to populations in North America.

**DIAGNOSIS.** Muzzle elongate (Fig. 1); tufts of whitish to pale grayish hairs on forearm; calcar longer than tibia, nearly half length of forearm; interfemoral membrane furred dorsally to exertion of tail; no wing sac. Upper incisors minute, simple, distinctly separated from each other and from canines; first upper premolar relatively large and slightly triangular in occlusal view, nearer canine than last premolar; rostrum deep posteriorly, virtually no angle between rostrum and braincase; basisphenoid pits deep, with well-defined outer borders but with no longitudinal ridge between them; maxillary tooththrows more or less parallel, breadth across molars equal to length of tooththrow (Husson, 1962; Miller, 1907a).

**GENERAL CHARACTERS.** This is a small bat, the forearm ranging from 35 to 41 mm in length and weight averaging about 4 g. The dorsum is grizzled brownish to grayish, with two faint whitish stripes on the lower back and rump; the venter is pale brownish gray. The pelage is soft and dense. The membranes and ears are dark brown. The prominent ears are narrowly rounded distally as is the tragus (Fig. 1). Mean external measurements (mm) for males ( $n = 46$ ) and females ( $n = 38$ ) from northern South America are, respectively: total length, 56.48, 59.18; length of head and body, 41.09, 42.34; length of tail, 15.39, 16.84; length of hind foot, 7.18, 7.45; length of ear, 13.20, 13.63; length of forearm, 36.87, 38.57; weight (g), 3.80, 3.99 (Eisenberg, 1989). Weights of pregnant females have been recorded to 6.0 g (Bradbury and Emmons, 1974). Length of the tragus is about 3 mm. Ranges in representative cranial measurements (mm) of five males, followed by those of four

females, from Suriname (Husson, 1962) are: greatest length of skull, 11.4-12.0, 11.6-12.0; condylobasal length, 10.1-10.6, 10.2-10.6; zygomatic breadth, 6.7-7.1, 6.7-7.2; breadth of braincase, 5.8-6.2, 6.0-6.3; height of braincase, 5.2-5.4, 5.1-5.3; mastoid breadth, 6.3-6.6, 6.3-6.6; postorbital constriction, 2.3-2.5, 2.2-2.4; breadth across molars, 3.8-4.5, 4.3-4.7; length of maxillary tooththrow, 4.2-4.4, 4.2-4.4; length of mandibular tooththrow (c-m3), 4.3-4.5, 4.3-4.4.

In the cranium (Fig. 2), the premaxillaries are broad posteriorly and terminate on the upper surface of the rostrum. The rostrum is slightly more than half the length of the braincase, and the lacrimal region is slightly inflated. The postorbital processes are well developed and slightly recurved. The auditory bullae are relatively large. The mandible rises abruptly posterior to the lower tooththrow. The lower incisors are trifid, forming a continuous arcade between canines. M1 has a conspicuous anteroexternal cusp that is distinct from the small parastyle. M1 and M2 have a distinct, subterete hypocone; M3 has a well-developed metacone and three commissures. Lower molars are similar in form, the third the smallest. The dental formula, as in all American emballonurids, is  $i\ 1/3, c\ 1/1, p\ 2/2, m\ 3/3$ , total 32 (Husson, 1962; Miller, 1907a; Sanborn, 1937). A relatively large baculum is present (Brown et al., 1971).

**DISTRIBUTION.** Tropical lowlands (infrequently above an elevation of 300 m) from southeastern México (northern Veracruz, eastern Oaxaca, and the base of the Yucatán Peninsula) southeastward through Middle America into much of the northern half of South America (Fig. 3), south of southeastern Brazil and, east of the Andes, to Perú and northern Bolivia (Hall, 1981; Koopman, 1982). There is no known fossil record for this species.

**FORM AND FUNCTION.** The baculum of *R. naso* is considerably larger than that of any other North American emballonurine (*Balantiopteryx*, *Cormura*, *Peropteryx*, and *Saccopteryx*) examined and figured by Brown et al. (1971). "In dorsal aspect, the baculum of this species flares outward from the base, narrows medially, and expands toward the rounded distal end. In lateral aspect, the basal end is concave, the central portion irregularly constricted, and the blunt end enlarged" (Brown et al., 1971:458-459). They reported the greatest length of the baculum as 0.80 mm and the greatest breadth at the base as 0.30 mm.

The stomach of *R. naso* possesses an elongate terminal portion between the gastroesophageal junction and pyloric sphincter, the increased length apparently related to food intake (Forman, 1971).

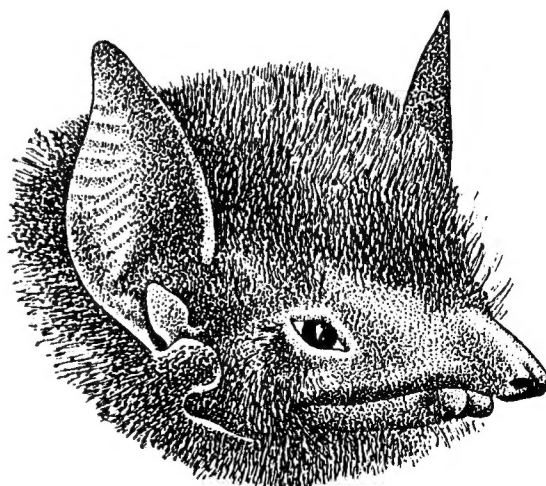


FIG. 1. Head of *Rhynchonycteris naso* (after Husson, 1962).



FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of lower jaw of *Rhynchonycteris naso* from Trinidad (male, Texas Tech University 5317). Greatest length of skull is 11.8 mm. Photograph by N. L. Olson.

Based on two specimens from Nicaragua, measurements of the stomach (mm) are: greatest length, 7.4–8.1; greatest breadth, 3.1–3.8; gastroesophageal junction to pyloric sphincter, 2.4–2.9; gastroesophageal junction to apex of fundic caecum, 2.5–2.8; breadth of pylorus at sphincter, 1.3–1.4 (Forman, 1972). The stomach is tubular, reniform, tapering from fundic caecum to pylorus; terminal endpiece lateral to the pyloric curvature is relatively long (2.5 mm). A cardiac vestibule is present, although short and narrow; the zone of incisura cardiaca is relatively deep and narrow, with no apparent separation of circular fibers into laminated sheets at incisura; the fundic caecum is well developed, dilated, expanded superiorly, and with the surface rounded throughout, and is structurally continuous with the midstomach. The pyloric sphincter is long and narrow. The musculature is generally thin throughout much of the stomach wall, but is thickened locally. Rugal folds are numerous and glands of Bruner are moderately abundant. The mucosal lining is reduced throughout much of the fundic caecum and greater curvature. The stomach conforms in most features and in general configuration to those of other obligate insectivorous bats; the fundus is variable in structure (Forman, 1972). *R. naso* has six Peyer's patches in the small intestine (Forman, 1974), covering an average of 6.5 mm<sup>2</sup> ( $n = 2$ ).



FIG. 3. Geographic distribution of *Rhynchonycteris naso* (after Hall, 1981, and Koopman, 1982).

Studies of aerodynamics (Findley et al., 1972; Lawlor, 1973) suggest that *Rhynchonycteris naso*, like many other emballonurines, is highly maneuverable in flight and probably can negotiate crowded spaces, enhancing aerial capture of small insects. Aspect ratio of the wing (6.54) and wing loading (0.045) were intermediate in scoring among 25 neotropical bats of several families (Lawlor, 1973).

Phillips and Jones (1969) found five developmental abnormalities (several figured) in the dentitions of 72 adults of *R. naso*: an unshed right upper deciduous incisor; an unshed third lower incisor on the left side in place of the permanent tooth; a supernumerary first upper premolar on the left and a supernumerary premolar between the left lower first and second premolars; a missing first upper premolar on the right side. Additionally, 10 specimens had dental abnormalities because of disease or mechanical damage. Burt and Stirton (1961) also reported an adult female that retained one milk incisor and a young adult male that had three. Sanborn (1937) and Goodwin (1942) discussed morphological variation in the first upper premolar in relation to intraspecific variation in this species. *Rhynchonycteris* has a small brain relative to body weight, a situation more or less typical of insectivorous species (Pirlot and Stephan, 1970); *R. naso*, however, has one of the lowest ratios of body weight (3.7–4.3 g) to brain weight (90–120 mg), the index of encephalization being 103 (see also Pirlot, 1969).

*Rhynchonycteris naso* develops a placental hematoma shortly after implantation, and the hematoma achieves its greatest development in late placental stages (Wimsatt and Gopalakrishna, 1958). The definitive hematoma occupies a position on the mesometrial side of the uterus, near the apex of the uterine cornu, and directly overlying the insertion of the ligamentum ovarii proprium. The attachment of the umbilical cord is always excentric and occurs on the side of the allantoic placental disc adjacent to the hematoma. From the exocoelomic aspect, the hematoma resembles an elongate ovoid sac, with the narrow end directed toward the root of the umbilical cord. It is about 3–5 mm long, 2–4 mm wide, and 1–3 mm thick. The hematoma in *R. naso* is similar to the placental hematoma in other mammals, except for differences in histological organization and development. This bat has a short umbilical cord (Wimsatt, 1960).

**ONTOGENY AND REPRODUCTION.** Females bear a single offspring per pregnancy. Unlike some sympatric emballonurids, *R. naso* inhabits a stable, relatively nonseasonal environment, and parturitions are asynchronous (Bradbury and Vehrencamp, 1977b). Relatively stable, year-round harems are formed (Hill and Smith, 1984). The age at first parturition of females is up to 18

months (Bradbury and Vehrencamp, 1976a). Number of pregnancies per individual female ranges from 0 to 2/year (Bradbury and Vehrencamp, 1976a, 1977b). Overlap of lactation following the first annual parturition and gestation with the second young is known. Aborted pregnancies were not observed by Bradbury and Vehrencamp (1977b).

This species evidently breeds throughout the year in at least some parts of its geographic range. In Middle America, pregnant females have been reported from January, February, and April from Veracruz, March from Belize (eight fetuses, 8–24 mm in crown-rump length), Guatemala (three fetuses, 4–23 mm), and Costa Rica, May from El Salvador, July from Tabasco, and August from Guatemala (Burt and Sturton, 1961; Dalquest, 1957; Dickerman et al., 1981; Dowler and Engstrom, 1988; Jones, 1966; Murie, 1935). Young were observed in April, May, June, July, and October in Costa Rica (Bradbury and Vehrencamp, 1976a), but not during the dry season (November to March), and in late May in El Salvador (Burt and Sturton, 1961). Immature animals and a lactating female were taken in Chiapas in July (Carter et al., 1966) and young have been recorded from April in Panamá and Veracruz (Allen and Barbour, 1923; Dalquest, 1957). Dalquest noted that females of each colonial group seemed to be in the same reproductive condition, but not in synchrony with those of nearby groups (he cited an instance where all females from one group were gravid, whereas all those from another at the same general locality were not). Colonies typically contain at least one female that fails to reproduce in a year (Bradbury and Vehrencamp, 1977b).

In South America, gravid females are on record from Trinidad in March, Ecuador in June, and Perú in July (Goodwin and Greenhall, 1961; Tuttle, 1970; Webster and Jones, 1984). Copulation was observed on Trinidad in July, and births were recorded from there in July and August (Bradbury and Emmons, 1974). A nursing young was taken in Bolivia in October (Anderson and Webster, 1983).

Little is known of the male reproductive cycle. Carter et al. (1966) reported a male with testes 4 mm in length from Chiapas in March. Webster and Jones (1980) took one in Bolivia in late July that had testes measuring  $3 \times 2$  mm. Dalquest (1957) reported measurements of  $2 \times 2$  and  $3 \times 3$  mm from Veracruz, but gave no dates.

Young are relatively large at birth, and begin to spend time away from (but nearby) their mothers within 1 week (Bradbury and Emmons, 1974); they reach adult size in about 2 weeks. Juveniles of both sexes disperse from parental groups to adjacent colonies after weaning, when 2–4 months old (Bradbury and Vehrencamp, 1976a, 1977b).

*Rhynchonycteris naso* inhabits localities in which there is little fluctuation in food availability over the year. Nonetheless, breeding may be timed to minimize risks to gravid females in terms of abundance of potential insect prey (Bradbury and Vehrencamp, 1977b), resulting in somewhat higher energy risks to dispersing young.

**ECOLOGY AND BEHAVIOR.** This common, colonial bat frequents areas near and over slow-moving watercourses (and occasionally lakes and swamps), and roosts in well-lighted areas. Colonies roost on the bark or roots of trees overhanging water, under bridges, at the mouths of caves over water, or under the curled dry leaves of the banana, *Musa*, or balisier, *Heliconia* (Goodwin, 1946; Goodwin and Greenhall, 1961), as well as on tree boles, rocks, and cliff sides near water (Bradbury and Emmons, 1974; Dalquest, 1957; Goldman, 1920; Hill and Smith, 1984; Husson, 1978), and in hollow logs (Dalquest, 1957). Allen (1935) reported *R. naso* was taken in a barn and under roof tiles, but these seem to us to be unlikely roosts for this species. In the Panama Canal Zone, colonies have been found roosting on lock gates of the canal and in abandoned concrete sentry boxes (Bloedel, 1955; Enders, 1935). On occasion, colonies may be found near swift-flowing streams, but in such cases usually in a relatively quiet backwater area, such as the mouth of an arroyo, rather than at streamside (Dalquest, 1957).

Murie (1935:17–18) wrote of *R. naso* in Belize as follows: “Along the upper reaches of the Belize River these bats, in groups ranging from six to thirty individuals, were noted on the under side of sloping trunks and root buttresses of large trees growing at the water’s edge. A few were observed on the sheltered parts of logs caught in snags, and a group of seven was found near the entrance of a shallow limestone cave facing the water. Generally these bats rest about six feet from the surface of the water.” Murie went on to note: “When frightened, a group would fly off together and alight

on a near-by tree similar to the one vacated. Both sexes were found together on the same tree.” Carter et al. (1966:489) reported the following about *R. naso*: “We have always found these bats associated with streams and rivers. They may be found roosting on a boulder at the edge of a stream, under a bridge but near the water, and on the trunks of trees that overhang or protrude from the water. Individuals select a more or less vertical surface for roosting and hang by the feet and thumbs. They are not uncommonly seen feeding along streams close to water, but they are not easily caught since they fly slowly and are so light in weight that they are not readily entangled when they strike a mist net. They are quick to fly when approached during the day.”

In Venezuela, Handley (1976) captured *R. naso* in mist nets (58%), and at roosts on logs (21%), on trees (15%), and on rocks (6%). Most captures (97%) were made in moist areas near or over streams. Evergreen forest provided 71% of captures, pastures and yards 18%, swamps 6%, and thorn forests 5%. Roost availability probably does not influence inter-colony spacing (Bradbury and Vehrencamp, 1976b), and thus is not likely a limiting factor. There is a well-defined space between each roosting bat. Members of large colonies usually roost in an oval pattern, sometimes divided into smaller clusters (Bradbury and Emmons, 1974). In smaller groups, individuals roost linearly, suggestive of a hierarchy, with spaces of 20–100 mm between individuals (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976a; Dalquest, 1957; Husson, 1978). Protective coloration makes individuals difficult to see against tree bark (Dalquest, 1957; Bradbury and Vehrencamp, 1976a), although they do roost against pale-colored surfaces as well. Single individuals occasionally are found (Dalquest, 1957), and night roosts also are known.

Due to its coloration, size, and roosting patterns, the Brazilian long-nosed bat has been mistaken for patches of lichens (Dalquest, 1957; Hill and Smith, 1984) or cockroaches (Dalquest, 1957). Predation at day roosts was not witnessed on Trinidad or in Costa Rica and was not suspected of limiting population densities there (Bradbury and Vehrencamp, 1976b). Husson (1962) reported predation on *R. naso* by hawks (*Buteo*) and falcons (*Falco*). Egrets (*Leucophoyx*) reportedly also take these bats (Sanderson, 1941). The annual survival rate of adult females was calculated to be at least 79% (Bradbury and Vehrencamp, 1977b).

Bright sunlight appears not to disquiet this bat, and individuals sometimes fly during the day (Bloedel, 1955; Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976a; Dalquest, 1957). They occupy well-lit, exposed roosts, and lack conspicuous displays or calling behaviors common to cavity-roosting species (Bradbury and Vehrencamp, 1976b). When disturbed, the group takes flight, weaving in linear formation to another roost, or, if scattered, individuals return after a time to the original roost (Dalquest, 1957). Goodwin and Greenhall (1961) reported that *R. naso* does not roost in association with other bats. Evidently this usually is the case, but several were captured with a specimen of *Thryoptera albigaster* in curled leaves of *Heliconia* in Panamá (Allen and Barbour, 1923), and *R. naso* associated with *Carollia brevicauda* and *C. perspicillata* in roosts in eastern Perú (Graham, 1988). Like bats in the genera *Saccopteryx* and *Peropteryx*, this bat places its wings at a 45° angle from its body while resting (Goodwin and Greenhall, 1961). Individuals hold the anterior portion of the body at a 20° angle to the roosting surface (Bloedel, 1955; Dalquest, 1957). Daily activity at the roost is minimal, but synchronized grooming periods occur, as do frequent periods of gentle rocking or swaying, although the reason for the latter activity is unknown (Bradbury and Emmons, 1974).

Colonies normally range in size from three to 45 individuals (Bradbury and Vehrencamp, 1976a, 1976b), but the usual number is five to 11 (average 7.8 bats/colony at one site in Costa Rica). However, one colony that “numbered about 100 bats” was found in each of 3 years in Veracruz (Dalquest, 1957:221). Colonies have from three to six roosting sites, to which they fly as a unit at intervals and when disturbed (Bradbury and Vehrencamp, 1976a). Females with young do not roost away from the main colony, but reproductive and nonreproductive females remain separated within a colony (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976a). Dalquest (1957:266), however, found females with nursing offspring roosting in a hollow log in Veracruz and opined that “the ordinary daytime resting place . . . is too hazardous for females with young.” He pointed out that roosts over water would result in young being drowned if they lost their grasp on their mother, and that females

with young frightened from the roost likely also would fall into water because they would be unable to fly with a heavy offspring attached. Thus, at this time, "they inhabit hollow logs lying on the ground."

Although adult males and females tend to be present in nearly equal numbers in colonies, there is always a dominant, adult male, which tends to be more continuously resident than others. This individual may return to the day roost even at night, whereas other males rarely do. The dominant male copulates in roosting groups without interruption. Population densities for combined roosting and foraging habitats in Costa Rica average about 8/ha (range, 3.6–11.2—Bradbury and Vehrencamp, 1976a, 1976b). Female reproductive hierarchies may exist, resulting in breeding only by mature adults—although it has been suggested that females may become reproductively mature at a later age than in some other emballonurines (Bradbury and Vehrencamp, 1976a). Older, reproductively active females forage in central, prey-rich patches, forcing younger, nulliparous females into less rich, solitary beats. "Two such beats, one of a nonreproductive female and one a male other than the most-resident bat, were both about 30 × 30 m in size" (Bradbury and Vehrencamp, 1976a:357).

Foraging begins at late dusk. *R. naso* feeds exclusively on insects (Albuja, 1983; Allen and Barbour, 1923; Dalquest, 1957; Goodwin and Greenhall, 1961), including chironomids and mosquitos, as well as small beetles and caddis flies. The bats probably prey on insects of appropriate size that are in greatest abundance within their foraging area (Bradbury and Vehrencamp, 1976a).

*Rhynchonycteris naso* forages almost entirely over water, from just above the surface up to a height of about 3 m. Polygonal foraging ranges in Costa Rica averaged 1.1 ha (range, 0.9–1.2—Bradbury and Vehrencamp, 1976a, 1976b). This bat favors rivers with a moderate flow (Dalquest, 1957; Bradbury and Vehrencamp, 1976a) and shallow depth, but may move away when waters on favored foraging areas are swelled by rain (Bradbury and Vehrencamp, 1976a). Colony-specific annual foraging ranges are maintained. Specific foraging sites are partitioned into colonial groups; breeding females and recent young feed as a group in a central part (or core) of the area, whereas males and younger females feed in solitude at the periphery. Bradbury and Vehrencamp (1976a:357) reported that in one colony "as many as six individuals could be found foraging within an area of only 4–5 m in diameter. Tandem flight paths, often with only 1 m between individuals, were frequently seen in these core areas."

The dominant, resident adult male often forages at the boundary of the feeding zone and chases intruding conspecifics from neighboring colonies (Bradbury and Vehrencamp, 1976a), using aerial attacks and audible vocalizations. When females of a foraging group move to new feeding areas, the resident male attends them with no interference from solitary, subdominant males occupying that area. When females return to the roost at night, the resident male again follows them, demonstrating that males of *R. naso* exhibit a primary pattern of female defense rather than resource defense (Bradbury and Vehrencamp, 1977a). Because defense of the colony foraging site is left to the single dominant male, increasing group size would not improve the potential defense of the foraging resource (Bradbury and Vehrencamp, 1976b). In Costa Rica, use of a particular foraging site by a colony averaged 4–6 weeks, with distances between new foraging sites ranging from 25 to 180 m (Bradbury and Vehrencamp, 1976a).

Foraging ranges and prey items overlap with those of the larger *Saccopteryx bilineata*, but the two species do not partition food resources altitudinally. However, *R. naso* and *Saccopteryx leptura*, which are of similar size, partition foraging sites by altitude (Bradbury and Vehrencamp, 1976a). *R. naso* occupies smaller foraging areas than sympatric species, which is accomplished by foraging over water in areas of high patch richness (Bradbury and Vehrencamp, 1976b).

Sonar pulses of this bat show a harmonic composition, with most energy concentrated in the second harmonic. The frequency of the pulses ranges from 80–105 kHz (Bradbury and Vehrencamp, 1976a). There is no frequency modulation (Novick, 1963).

Ectoparasites that occur on *R. naso* include (Brennan and Reed, 1975; Herrin and Tipton, 1975; Ueshima, 1972; Wenzel, 1976): *Hesperoctenes fumarius*, a polycatenid hemipteran; *Strebla hirsutus*, *Trichobius caecus*, and *T. longipes*, streblid batflies; *Eutrombicula variabilis* (Trombiculidae) and *Periglischrus iheringi* (Spinturnicidae), acarine mites. Specimens of *R. naso* examined from Trinidad were rabies-negative (Goodwin and Greenhall 1961).

**GENETICS.** This species has a chromosomal diploid number of 22. The fundamental number of 36 is the smallest among the species of emballonurids studied by Hood and Baker (1986); the X and Y chromosomes both are acrocentric. *Rhynchonycteris* shares a banded element with the Old World *Taphozous* that is otherwise unknown in New World genera. It also is unique in having an interstitial C-band on the largest acrocentric chromosome (Hood and Baker, 1986).

**REMARKS.** The generic name is a combination of the Greek words *rhynchos* and *nykteris*, meaning nose or snout and bat, respectively. The specific name is from the Latin *nasus*, which also refers to nose. Some of the other vernacular names that have been applied to this bat include Mexican long-nosed bat, proboscis bat, Jacob's ladder bat, tufted bat, sharp-nosed bat, and (Spanish) *murciélaguito narigón*.

Based on electrophoretic and immunologic studies of Emballonuridae, *Rhynchonycteris* should be classified with all other New World genera in the morphologically diverse tribe Diclidurini, subfamily Emballonurinae, because these genera "form a monophyletic unit both morphologically and biochemically" (Robbins and Sarich, 1988:11).

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